ALLOMETRIC SPACE AND ALLOMETRIC DISPARITY: A DEVELOPMENTAL PERSPECTIVE IN THE MACROEVOLUTIONARY ANALYSIS OF MORPHOLOGICAL DISPARITY

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Here, we advance novel uses of allometric spaces—multidimensional spaces specifically defined by allometric coefficients—with the goal of investigating the focal role of development in shaping the evolution of morphological disparity. From their examination, operational measures of allometric disparity can be derived, complementing standard signals of morphological disparity through an intuitive and process-oriented refinement of established analytical protocols used in disparity studies. Allometric spaces thereby become a promising context to reveal different patterns of evolutionary developmental changes and to assess their relative prevalence and importance. Such spaces offer a novel domain of investigation of phenotypic variation and should help in detecting large-scale trends, thus placing various macroevolutionary phenomena in an explicitly developmental context. Ammonoidea (Cephalopoda) at the Lower-Middle Jurassic transition were chosen as a case study to illustrate this methodological approach. We constructed two phenotypic spaces: a static, adult one (adult morphospace) and a dynamic, developmental one (allometric space). Comparative disparity analyses show a strikingly stable occupation in both spaces, despite extensive change in taxonomic composition. In contrast, disparity analyses of subclades reveal clearly distinct morphological and allometric disparity dynamics. Allometric approaches allow developmental insights into morphological diversification otherwise intractable from the analysis of adult morphospace alone.

KEY WORDS: Allometry, ammonites, development, macroevolution, morphospace, morphometrics.

Over the last two decades, the concept of morphological disparity (Gould 1989a, 1991; Foote 1997), that is, the morphological signal of biodiversity, has proved to be an invaluable source of information, complementing taxonomic approaches, and enriching our knowledge of large-scale clade dynamics in both paleo- and neontological contexts (e.g., Foote 1991, 1993a, 1995, 1997; Ricklefs and Miles 1994; Wills et al. 1994; Dommergues et al. 1996; Roy and Foote 1997; Eble 2000; Roy et al. 2001; Neige 2003; McClain et al. 2004; Navarro et al. 2005; Ricklefs 2005). Current analyses of morphological disparity, now widely applied, are focused on characterizing morphospace and its differential occupation through space and time.

Hypotheses about processes responsible for documented disparity patterns have mostly been cast in terms of external factors, whereas potential developmental explanations have received much less attention (Eble 2003; McNamara and McKinney 2005). This results in large part from the fact that most morphospaces and disparity studies have traditionally emphasized sampling of adult shapes. More extensive consideration of the developmental aspects underlying the emergence of these adult forms

is now needed to allow a broader and more balanced array of inferences.

Attempts to infer connections between developmental dynamics and disparity dynamics can for instance be found in David (1990), Hugues (1991), McShea (1993), Wagner (1995), David and Laurin (1996), Neige et al. (1997a), Eble (1998, 2000), and Ciampaglio (2002). In recent works (Eble 2002, 2003; Zelditch et al. 2003; Gerber et al. 2007), adult disparity is contrasted with the disparity of their related juvenile forms. These clade-wide disparity comparisons, when combined with statistical analyses of ontogenetic trajectories, allow the detection of changes in disparity through ontogeny, thus helping quantitatively assess the role of development in shaping morphospace occupation and adult disparity. Nevertheless, there is still no comprehensive quantification of the variety of ontogenetic trajectories per se, and no explicit measure to track it over geological time. In this article, we advance an explicitly allometric approach to address this issue.

Allometry—the study of size-related shape changes (Huxley 1932; Huxley and Tessier 1936; Jolicoeur 1963; Cock 1966; Gould 1966; Mosimann 1970; Sweet 1980; see Gayon 2000 for a historical review)—presents itself as an operational framework to place disparity in a developmental context, inasmuch as paleobiology's focus on development is essentially organismal and almost always with unavailable age data (Jones and Gould 1999).

Here, we propose the relevance of allometric data as a basis for the establishment of an additional phenotypic space—the space of allometric coefficients (allometric space)—complementing usual adult morphospace. Its developmental content allows the appraisal of the disparity of ontogenetic trajectories (allometric disparity).

Methods

The approach outlined below supplies a multivariate ordination of taxa based on their allometric trajectories and a quantitative appraisal of their developmental disparity. Allometric coefficients can be derived from either traditional or geometric morphometrics. The method is here described in the context of traditional multivariate allometry (distance-based measurements; cf. case study below), but all analyses and inferences apply as well for size and shape data based on geometric similarity (Mosimann 1970; Klingenberg 1998).

Under the concept of Huxley's (1932) simple allometry and its multivariate generalization, which holds for many organisms, an ontogenetic trajectory appears as a straight line in the space of log-transformed measurements. Following Jolicoeur (1963), the direction of this line is best estimated by the first principal component of the covariance matrix of the log-transformed measurements (principal component analyses carried out separately for each taxon). The allometric pattern of each taxon is thus described by a vector of first principal component coefficients providing a synthetic characterization of the multivariate pattern of allometric growth. All these vectors can then be treated as observations in a new dataset expressing the variation among multivariate allometric patterns in the space spanned by allometric coefficients (Solignac et al. 1990; Klingenberg and Froese 1991; Klingenberg 1996). We further refer to this space as the allometric space (a developmental morphospace sensu Eble 2003). Main information in allometric space can be extracted via principal component analysis performed on the covariance matrix of the allometric patterns. Note that each taxon in the allometric space is represented as a point summarizing its allometric trajectory, whereas a point in usual morphospace corresponds to a shape sampled on this allometric trajectory at a given size or age.

Distance among specimens in morphospace is a central issue in disparity analyses and many disparity metrics are estimates of average intershape distance. Likewise, distances in allometric space are developmentally informative. For two taxa described by their normalized vectors of allometric pattern a and b, the distance d_{a-b} between them in the allometric space is related to the angle between their directions in the space of log-transformed measurements.

$$d_{a-b} = \sqrt{2(1 - \cos(\alpha))}$$

With α the arc cosine of the dot product of the two vectors

$$\alpha = \arccos(a.b^T)$$

Isometry—the maintenance of geometric similarity with size increase (e.g., Gould 1966)—can also be depicted in the allometric space. The isometry vector is a p-length vector with all coefficients equal to $p^{-1/2}$, corresponding to a growing organism whose proportions remain constant (Jolicoeur 1963). The isometry vector supplies both a reference for assessing the degree of allometry of a given trajectory according to its distance to isometry, and a way to polarize ontogenetic change between ancestor and descendant (Klingenberg 1998).

In the case of simple allometry, evolutionary changes in ontogeny can be ascribed to three different phenomena: (1) Lateral transposition (LT), that is, a translation in space of log-transformed measurements, (2) ontogenetic scaling (OS), that is, an extension or a truncation of the ancestral trajectory, (3) change of slope (CS), that is, a loss of parallelism of trajectories between ancestor and descendant (e.g., Shea 1985; Klingenberg 1998). Note that only CS alters the structure of the covariance matrix of a taxon and thus its allometric pattern. Hence, taxa whose trajectories statistically differ only by LT or OS will share a common allometric pattern and will appear merged in allometric space.

The next step consists in quantifying allometric space occupation. An advantage of the approach proposed in this article is that

all quantitative methods developed in the context of morphospace disparity analysis can be directly and meaningfully transposed to the exploration of allometric spaces. Classical disparity metrics include total variance and total range (e.g., Foote 1997). Total variance (sum of univariate variances) is a measure of spacing of taxa in state space. In morphospace, it is proportional to the average dissimilarity among forms (intershape distance) and is computed as the trace of the covariance matrix of shapes variables. In allometric space, it is computed as the trace of the covariance matrix of allometric patterns and is proportional to the average angle among allometric trajectories (degree of parallelism in the bundle of trajectories). Total range (sum of univariate ranges) quantifies the spreading of taxa in morphospace and can also be applied to allometric space. Because this metric is sample-size dependent a rarefaction procedure is required (Foote 1992).

We propose the average distance to isometry as an additional disparity metric specifically devised for allometric space. This is the average distance in the allometric space between allometric patterns of occurring taxa and the isometry vector, that is, the average angle between the isometric growth and the bundle of allometric trajectories. Contrary to the two previous metrics, average distance to isometry incorporates positional information because location of isometry is fixed in allometric space. Thus, shifts in allometric space can alter allometric disparity measured in relation to isometry without necessarily modifying variance- or range-based estimates.

CASE STUDY: the Lower-Middle Jurassic transition in ammonites (Cephalopoda)

Context and Data

As an empirical illustration of this approach, we present an example based on the Lower-Middle Jurassic transition in ammonites. This work can be seen as the addition of a developmental perspective to a recent study by Neige et al. (2001), which only focused on quantification of adult morphological disparity.

Ammonites have already and successfully been submitted to morphological disparity analyses at various temporal and taxonomic scales (Saunders and Swan 1984; Dommergues et al. 1996; Neige et al. 1997b; McGowan 2004; Saunders et al. 2004; Villier and Korn 2004; Navarro et al. 2005; Moyne and Neige 2007). Here, ammonites are particularly suitable: They can be efficiently described with few morphometric traits (e.g., using Raup's [1966, 1967] model for shell shape); furthermore, because the shell contains a record of the entire growth, ammonites can be advantageously used for addressing ontogeny-oriented issues (e.g., the use of longitudinal data; Cock 1966).

Neige et al. (2001) emphasized the modalities of ammonite morphological evolution at the Lower-Middle Jurassic boundary,

marked by a deep taxonomic renewal (ammonite family Hammatoceratidae replacing Graphoceratidae) and sometimes questioned as an extinction event (Sandoval et al. 2002). The main pattern they documented was an increase in morphological disparity throughout Lower Jurassic, and its stagnation thereafter, suggesting that this Jurassic transition might be part of a larger event initiated earlier. Ammonite taxonomic diversity in this period displayed a moderate increase during Lower Jurassic, followed by a decrease and stabilization around the initial diversity level.

In our analysis, paleogeographic context, temporal resolution, and taxonomic sampling are similar to Neige et al. (2001). Sixty-three species are studied, belonging to five families (Graphoceratidae, Hammatoceratidae, Hildoceratidae, Phylloceratidae, and Lytoceratidae) and spanning seven ammonite subzones (Last two zones of Lower Jurassic and first zone of Middle Jurassic, i.e. ~2 MYA).

Adult Morphospace and Allometric Space

We measured a total number of 699 specimens, that is, some 10 specimens per species, which, given the relative simplicity of ammonites allometric trajectories, provide a rather accurate depiction of shell growth for each species.

Three linear measurements (diameter D, radius R, and whorl height Wh; Fig. 1) suffice to obtain a reasonable representation of shell lateral shape using Raup's (1967) parameters D_R and W_R:
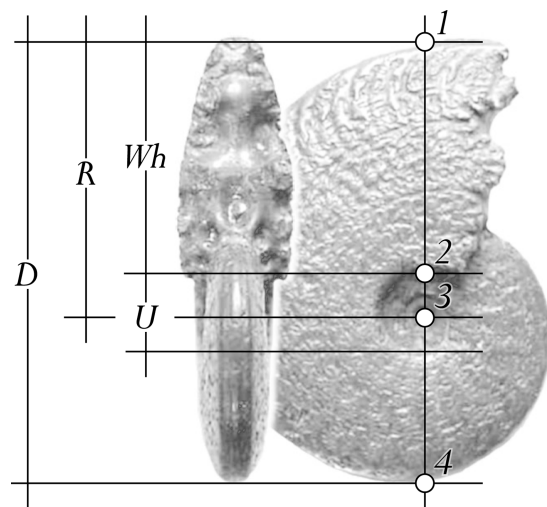

Figure 1. Morphometric scheme of ammonoid shell. Four linear measurements are taken on the shell: shell diameter D, umbilical width U, radius R and whorl height Wh; D, R and Wh serve as input for calculation of Raup parameter D_R and W_R. These raw variables can also be envisioned as a set of four collinear landmarks [0, Wh, R, D], analyzed via standard geometric morphometric methods (see text), providing reliable measure of intershape distance (Procrustes distance) used here for computation of disparity estimates.

$$D_R = (R - Wh)/R$$

$$W_R = (R/(D - R))^2$$

Average adult shape (shape at adult size) for each species is obtained from multivariate linear regression of log-transformed variables Wh and R on log D. Adult size is measured as the diameter of the mature phragmocone, which is determined using the septal approximation criterion (Bucher et al. 1996). Most of these adult size estimates have been recently compiled and analyzed in a study of Lower Jurassic ammonites (Dommergues et al. 2002).

For the analysis of multivariate allometry, we also measure umbilical width (U) to enrich our description of allometric trajectories in the space of linear measurements. As mentioned above, we compute vectors of allometric pattern as the first principal components of the covariance matrices of log-transformed measurements for each species.

Morphological and Allometric Disparity Analyses

Although adult morphologies are visualized in the $W_R - D_R$ plane of Raup morphospace, adult disparity computations have been done in tangent Procrustes shape space (geometric morphometrics), providing a reliable measure of intershape distance for disparity analyses. Briefly, linear measurements are used to build vectors of coordinates $[0, Wh, R, D]$ corresponding to a set of four collinear landmarks (Fig. 1). These one-dimensional landmark data are then submitted to generalized Procrustes analysis (Rohlf and Slice 1990). It supplies a spherical shape space identical to the preshape space because no rotational fit is required (see Small 1996 for details). Because of the limited amount of empirical shape variation, tangent approximation provides a reliable representation of intershape distances ($r > 0.999$ here; Rohlf 1999).

We use total variance and rarefied total range as metrics of disparity in both adult morphospace (standard morphological disparity) and allometric space (allometric disparity), as well as the average distance to isometry for complementing allometric space analysis.

Relative contributions of ammonoid families to the global signal are assessed via partial disparity analysis (only for variance-based metrics) following Foote's (1993b) additive partitioning of sums of squares. In this approach, the partitioning differs from that of ANOVA (e.g., Sokal and Rohlf 1995) so that disparity components sum up to total disparity.

Results

Adult "static" morphospace and allometric "dynamic" space are presented in Figure 2. Distribution of the sample in Raup morphospace outlines the broad global morphological diversification of ammonoids in Lower and Middle Jurassic (see Raup 1967 and Ward 1980 for comparisons). In the allometric space, the spectrum of allometric variation is almost unidimensionnal and its first component summarizes almost all of the original variance (>90%; Fig. 2). It simply reflects the two extreme possible ontogenetic alternatives for coiled shell displaying allometric growth: from evolute- to involute-shaped shell, or the converse. Analyses of taxa distribution within morphospace reveal an almost even occupation for both disparity indexes, except a slight decrease in the first two subzones (Fig. 3). This counterintuitive pattern, given the deep taxonomic renewal and the changes in standing diversity, is also found in the allometric space where no significant variation of allometric disparity can be detected.

Because of their peripheral location in morphospace, and their morphological conservatism, Lytoceratidae and Phylloceratidae tend to stabilize global signals of morphological and
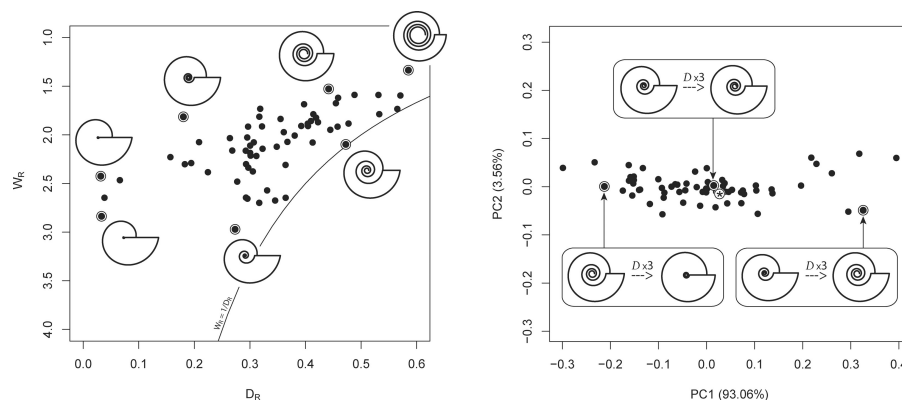
Figure 2. Adult morphospace (left) and allometric space (right) of ammonoids at the Lower-Middle Jurassic transition. Adult morphospace is visualized in the $D_R - W_R$ plane of Raup space and extreme morphotypes are pictured. Allometric space shows the distribution of allometric patterns of the same taxa. Each allometric trajectory is displayed as a point. The closer to isometry (encircled star) the less allometric the growth is (shape changes illustrated for triplication of shell diameter).
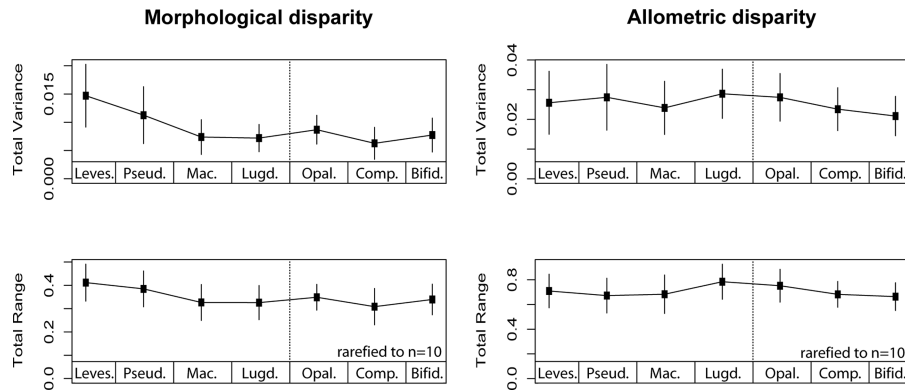
Morphological disparity

Allometric disparity

Figure 3. Curves of morphological and allometric disparity for ammonoids based on variance- and range-based metrics. Error bars are bootstrapped standard errors (1000 replicates). Dashed line marks the Lower-Middle Jurassic transition. Ammonite subzone labels: Leves. (Levesquei), Pseud. (Pseudoradiosa), Mac. (Mactra), Lugd. (Lugdunensis), Opal. (Opalinum), Comp. (Comptum), Bifid. (Bifidatum).

allometric disparity. Therefore, we also performed disparity analyses only focusing on ammonitina families Harpoceratidae, Hildoceratidae, and Hammatoceratidae (∼85% of the whole dataset; Fig. 4).

Because the isometry vector is located near the origin of the allometric space (i.e., the average allometric pattern of Ammonitina is isometry), as do centroids of each subset of allometric patterns across time (subsets remain roughly centered around the centroid of the whole set), total variance displays a disparity signal comparable to the average distance to isometry. This is purely coincidental and such redundancy may not necessarily occur in other empirical studies, as these two metrics focus on different aspects of space occupation.

Ammonitina morphological and allometric disparity patterns are more complex than global patterns (Fig. 4). Graphoceratidae family displays no major variation in average adult size through time (∼50mm) suggesting LT and/or CS to be more involved than

OS in morphological and allometric dynamics. Despite marked variations in allometric disparity (reflecting CS; e.g., increase in Lugdunensis subzone), variations in morphological disparity are weak. This suggests that magnitude of shape changes implied by CS is potentially smaller than magnitude implied by LT. LT thus seems to be the prevailing process in Graphoceratidae morphological evolution.

Morphological and allometric signals tend to be more correlated in Hammatoceratidae, at least in the first five subzones. Then, allometric disparity is almost exclusively generated by this family, whereas contributions to morphological disparity are comparable for the three Ammonitina families. As for Graphoceratidae, this pattern may be due to morphological evolution mainly driven by LT (perhaps more efficient than CS in modifying morphospace occupation), or to the severe decrease in average adult size (OS) in Middle Jurassic (from ∼150 to ∼75mm), which could have minimize the impact of unparallel trajectories on adult shape variation.

Morphological disparity

Allometric disparity
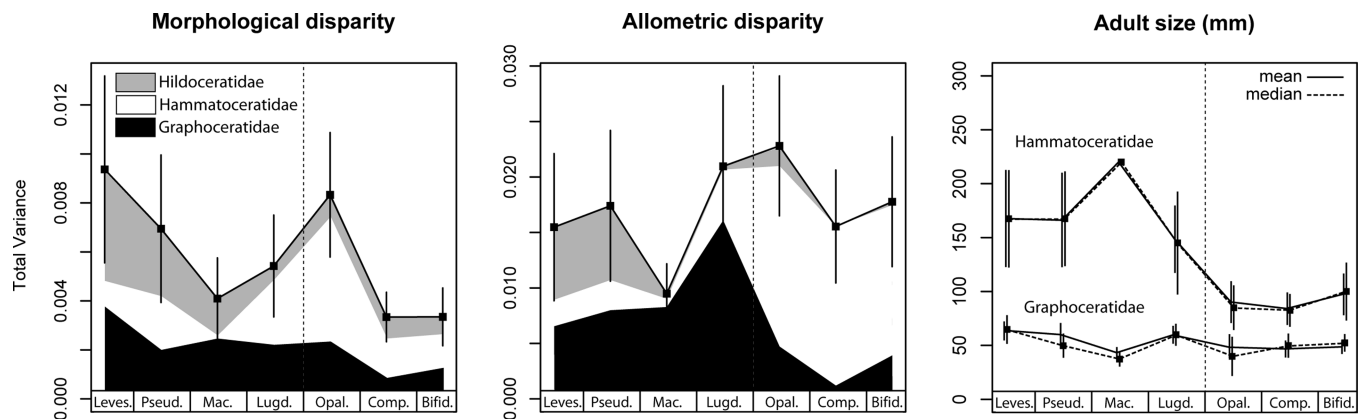
Adult size (mm)

Figure 4. Curves of morphological and allometric disparity of Ammonitina and contribution of Hildoceratidae, Hammatoceratidae and Graphoceratidae to the whole suborder (partial disparity analyses; additive partition of variance-based disparity). Curves of adult size of Hammatoceratidae and Graphoceratidae. Error bars are bootstrapped standard errors (1000 replicates). Dashed line marks the Lower-Middle Jurassic transition. For Ammonite subzone labels see legend of Figure 3.

First complementary analyses (e.g., inspection of morphological disparity in early ontogeny for testing morphological effect of LT) suggest a mixture of both hypotheses.

Interestingly, the Lower-Middle Jurassic transition is characterized by the replacement of Graphoceratidae by Hammatoceratidae, which forms the ancestral stock that led to the Middle Jurassic ammonite radiation (Moyne and Neige 2004).

Discussion

Allometric space seems to be a fruitful tool for investigating the role or the dynamics of development in empirical paleobiological studies. Allometric space is an ordination of taxa based on the allometric patterns of their ontogenetic trajectories. Allometric coefficients are obtained from morphometric analyses (traditional or geometric morphometrics) of ontogenetic data and serve as new variables defining the allometric space. In case of simple allometry (linear trajectories in space of log-transformed measurements), taxa are depicted as points in allometric space (cf. example above). For taxa displaying polyphasic log-linear allometry (trajectories divided into successive linear portions) or complex allometry (curvilinear trajectories), allometric patterns appear as several distinct points (virtually linked by segments corresponding to critical developmental periods) or as continuous curves (reflecting size-related changes of allometric patterns). Allometric space can be considered as an additional space that valuably complements our description of phenotypic evolution usually inferred from (adult) morphospace exploration.

In this article, we introduced the notion of allometric disparity—quantitative estimate of the variety of allometric designs in a clade—as a conceptual and analytical transposition of morphological disparity framework to allometric space. Allometric disparity is a biodiversity metric enlightening other aspects than taxonomic, phylogenetic or morphological metrics. As it has been shown in the case study, morphological and allometric disparities are not redundant: curves of morphological and allometric disparity in ammonites display different temporal patterns (see Fig. 4). Analytically, all indexes quantifying state-space occupation and designed in the disparity context can be directly applied to allometric space.

Over the past few years, disparity patterns have been documented for many clades and contrasted with traditional taxonomic proxies (curves of taxonomic diversity). Recurring patterns, concordance/discordance between morphological and taxonomic diversity, and temporal asymmetry of clade shape have enriched our knowledge of plausible underlying evolutionary mechanisms (Erwin 2007). Similarly, comparisons of allometric disparity—a possible proxy for developmental dynamics at large scale—with taxonomic and morphological signals are likely to refine our in-

terpretation of clade history in terms of temporal, phylogenetic, or ontogenetic trends.

As a complementary domain of phenotypic investigation in disparity analysis, morphometric descriptions of how diversity of adult shapes arises, that is, how allometric space occupation can drive morphospace structuration, allow mechanistic insights and inferences on occurring processes. For instance, the use of phylogenetic and geometrical references (ancestral taxa, isometry...) enables to detect paedo- or peramorphosis between related taxa even in the absence of age data. At larger taxonomic scale, average distance to isometry can be used to detect paedo- or peramorphocline. More generally, comparisons of morphological disparity, allometric disparity, and variations in average adult size provide simple ways to distinguish the presence of evolutionary changes such as LT, OS and CS of allometric trajectories. In the case study, discordances between morphological and allometric disparity indicate different evolutionary developmental changes among ammonite families (LT in Graphoceratidae vs. CS/OS in Hammatoceratidae, see Fig. 4). Further investigations applied to other clades should help assessing the relative frequencies of these processes and their differential ability to generate morphological disparity (e.g., in terms of magnitude of morphological transitions allowed). Because the developmental bases of these processes are undoubtedly different, frequency contrasts are informative regarding potential developmental correlates of differential clade dynamics.

Other analyses may include the study of allometric disparity at particular events of clade history such as evolutionary radiation, extinction, or post-crisis recovery. In the present study, the allometric description suggests a possible interpretation of Middle Jurassic ammonite history. Hammatoceratidae gave rise to all post-Lower Jurassic Ammonitina (Donovan et al. 1981; see also Moyne and Neige 2004 for a cladistic analysis). It has been shown here that Hammatoceratidae displayed a significantly greater allometric disparity than coexisting ammonite clades at the very beginning of the Middle Jurassic (see Fig. 4). This high allometric disparity level could be seen as a possible explanation for their subsequent radiation. Such relationships between allometric disparity and macroevolutionary dynamics could be statistically investigated in other clades and at various taxonomic levels.

To conclude, beyond the somewhat controversial diversification, complexification and reformulation of models, formalisms and terminology in the studies of ontogeny/phylogeny relations (Alberch et al. 1979; McKinney and McNamara. 1991; Klingenberg 1998; McKinney 1999; Gould 2000), documentation of macroevolutionary patterns of taxonomic diversity and morphological disparity with insights into underlying developmental dynamics remains an important issue. Consideration of ontogenetic information is fundamental for enlarging our understanding of macroevolutionary dynamics. Disparity analyses should gain

in integrating development as testable hypotheses and/or in devising operational tools allowing comprehensive empirical characterizations of its role. Even if not necessarily supplying the full causal explanation of the pattern observed, it may offer additional clues about the way phenotypic changes occur and details on the developmental mechanisms involved in morphological macroevolution.

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